

THE TRILOBITE *LEJOPYGE* HAWLE AND CORDA AND THE MIDDLE-UPPER CAMBRIAN BOUNDARY

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ABSTRACT. The species and subspecies of the late middle Cambrian agnostid trilobite *Lejopyge* are reviewed. *Lejopyge cos* Öpik is shown to be a junior synonym of *Lejopyge laevigata armata*. In Sweden the middle-upper Cambrian boundary is placed at the boundary between the *Lejopyge laevigata* and *Agnostus pisiformis* Zones. The reassignment of *L. cos* to *L. l. armata* and other criteria suggest that this boundary in Australia should be drawn within the Mindyallan *Cyclagnostus quasivespa* Zone between the *L. cos* and *Blackwelderia sabulosa* faunas.

It is suggested that the middle-upper Cambrian boundary in North America be placed well up into the *Cedaria* Zone; in China it is at some as yet undefined position within the *Blackwelderia sinensis* Zone; on the Siberian Platform it should be placed between the zones of *Lejopyge laevigata armata*-*Lomsucaspis alta* and *Agnostus pisiformis*-*'Homagnostus fecundus'*; and in north-west Siberia between the zones of *Maiaspis spinosa*-*Oidalagnostus trispinifer* and *Acrocephalella granulosa*-*Koldiniella proluxa*.

VARIOUS species and subspecies of *Lejopyge* are important index fossils of the late middle Cambrian of Sweden (Westergård 1946), Utah (Robison 1964*a, b*), Queensland (Öpik 1961*a*, 1967), Siberia (Demokidov 1968), and Alaska (Palmer 1968).

This paper reviews the status of the species and subspecies of *Lejopyge* and discusses the intercontinental correlations arising out of this work. The availability of large numbers of latex moulds and silicone-rubber casts of trilobites (especially those illustrated by A. H. Westergård from Sweden), allowed many conclusions to be drawn which otherwise could not have been made from the published literature.

Order MIOMERA Jaekel, 1909

Suborder AGNOSTINA Salter, 1864

Superfamily AGNOSTACEA M'Coy, 1849

Family AGNOSTIDAE M'Coy, 1849

Subfamily PTYCHAGNOSTINAE Kobayashi, 1939

Genus LEJOPYGE Hawle and Corda, 1847

Synonymy. *Lejopyge* Hawle and Corda, 1847, p. 51; Kobayashi 1937, pp. 437-447; 1939, p. 131; Lermontova 1940, p. 130; Westergård 1946, p. 87; Hupé 1953, p. 61; Pokrovskaya 1958, p. 72; 1960, p. 60; Howell 1959, p. 178; Öpik 1961*a*, p. 85; 1967, p. 93; Robison 1964*a*, p. 521; Palmer 1968, p. 27. *Miagnostus* Jaekel, 1909, p. 401.

Type species. *Battus laevigatus* Dalman, 1828, p. 136.

Discussion. Westergård (1946, p. 87) and Öpik (1961*a*, pp. 76, 85) have discussed *Lejopyge*, its species and subspecies, and its relationships with other genera, especially *Ptychagnostus* Jaekel. Westergård (1946, p. 75) suggested, and Öpik (1961*a*, p. 85) agreed, that *Ptychagnostus* (*Triplagnostus*) *elegans* (Tullberg), *P. elegans laevissimus* Westergård (Pl. 63, figs. 12, 13), and *L. laevigata* (Dalman) 'constitute an evolutionary series with very small intervals'.

The following species and subspecies have been included in *Lejopyge*: *L. calva* Robison, *L. cos* Öpik, *L. empozadensis* Rusconi, *L. exilis* Whitehouse, *L. laevigata* (Dalman), *L. laevigata armata* (Linnarsson), *L. l. forfex* (Brögger), *L. l. perrugata* Westergård, *L. l. rugifera* Westergård, *L. l. similis* (Brögger), and *L. obsoletus* (Kobayashi).

Öpik (1961a, p. 86) suggested that the holotype cephalon of *L. exilis* belongs in either *L. laevigata* or *L. l. armata* and that the pygidium of *L. exilis* figured by Whitehouse (1936, pl. 9, fig. 12) belongs in either *Phalacroma? dubium* Whitehouse or *Hypagnostus hippalus* Öpik. This pygidium is very poorly preserved (Pl. 63, fig. 11) and cannot be assigned to any species or genus with certainty. In our opinion the border is far too wide to include the specimen in *L. laevigata*. Westergård (1946, p. 88) suggested that *L. l. similis* belongs in *Cotalagnostus confusus* (Westergård), and that *L. l. forfex* resembles the pygidium figured as *L. l. armata* by Westergård (1946, pl. 13, fig. 31). The pygidium described by Kobayashi (1935) as *Aagnostus (Lejopyge?) obsoletus* was reassigned by him (Kobayashi 1962, p. 30) to *Phoidagnostus limbatus*. *L.? controversa* Kryskov (in Borovikov and Kryskov 1963) belongs in *Peratagnostus* Öpik (1967, p. 35). *L.? sugandensis* Kryskov was described in Borovikov and Kryskov (1963, p. 275, pl. 1, fig. 9). However, a footnote (p. 274) indicates reassignment of *sugandensis* to *Phaldagnostus* Ivshin.

Rusconi (1953, p. 5) described a single pygidium as *L. empozadensis*. He later redescribed and figured the same specimen (1954, p. 33, pl. 2, fig. 10) as *L. empozadense*. As far as can be determined from the figure, this species has a much wider border than any described species of *Lejopyge*. The specimen described and figured by Rusconi (1951, p. 8, fig. 9) as *Spinagnostus pedrensis* was later assigned by him to *L. pedrensis* (Rusconi 1953). However, the figure given by Rusconi (1951) is inadequate for either generic or specific identification.

Robison (1964a) described *L. calva* from Utah and Nevada where it is the nominate species of the youngest of the three subzones of his late middle Cambrian *Bolaspidella* Assemblage Zone. Palmer (1968) described *L. calva* from Alaska. *L. calva* is more effaced (Pl. 63, fig. 10) than *L. laevigata* and its subspecies.

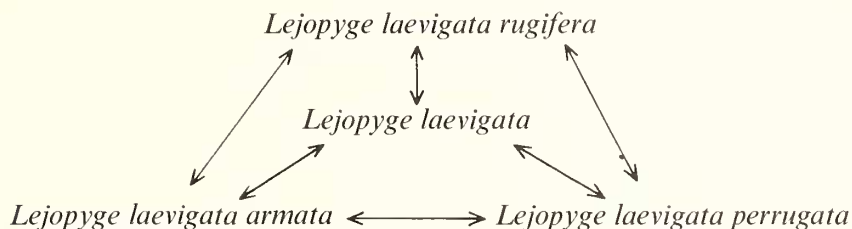
Robison (1964a, p. 522) reported the occurrence of an unnamed subspecies of *L. calva* from U.S. Geological Survey Collection 2523-CO from Schell Creek Range, Nevada, characterized by postero-lateral border spines on the cephalon, but not on the pygidium. A pygidium is figured (Pl. 63, fig. 9), but none of the available associated cephalons show undoubted cephalic spines. Cephalons and pygidia from a *Lejopyge-coquina* from Patterson Pass, Snake Range, East Nevada, are almost entirely effaced and are figured as *Lejopyge* sp. (Pl. 63, figs. 7 and 8) but may well be representatives of *L. calva*.

L. cos was described by Öpik (1967, p. 93) from the lower two zones (*Erediaspis eretes* and *Cyclagnostus quasivespa* Zones) of the Mindyallan Stage of north-west Queensland, which were placed in the upper Cambrian, thus making *L. cos* the youngest species of *Lejopyge*. All other described and authenticated species of *Lejopyge* come from late middle Cambrian horizons. As concluded below, we believe that *L. cos* is a junior synonym to *L. l. armata* and that it is of late middle Cambrian age.

L. laevigata and *L. l. armata* are differentiated on the basis of the latter having

cephalic and pygidial spines. However, there are small postero-lateral spines on the pygidium of *L. laevigata* (Westergård 1946, pl. 13, fig. 25; Pl. 62, fig. 10). There are also short spines on the cephalon of *L. laevigata* (Westergård 1946, pl. 13, fig. 24; Pl. 62, fig. 2). *L. l. perrugata* and *L. l. rugifera* were erected by Westergård (1946) for forms with cephalata showing a greater degree of scrobiculation than in either *L. laevigata* or *L. l. armata*. However, some of the cephalata of *L. laevigata* and *L. l. armata* illustrated by Westergård (1946, pl. 13, figs. 22, 35) are scrobiculate to varying degrees (Pl. 62, fig. 3). *L. l. rugifera* was differentiated from *L. l. perrugata* by Westergård on the basis of the latter having short cephalic spines with no mention of cephalic spines in the diagnosis of *L. l. rugifera*. The cephalic spines of the holotype of *perrugata* are quite large (Pl. 63, fig. 1) and the holotype of *rugifera* also has cephalic spines albeit short (Pl. 63, fig. 6). The pygidia (Pl. 62, figs. 12, 13; Pl. 63, figs. 2-4) associated with the holotype cephalata of *rugifera* and *perrugata* are indistinguishable from pygidia of *L. laevigata* and *L. l. armata*.

Westergård noted the great morphological variation within *L. laevigata* and also the presence of intermediate forms between *L. laevigata* and *L. l. armata*, *L. l. perrugata* and *L. l. rugifera*, and between the subspecies (see text-fig. 1). This variation and the presence of intermediate forms indicate that we are dealing with a species complex with the subspecies *armata*, *perrugata*, and *rugifera* representing extreme forms of *L. laevigata*.



TEXT-FIG. 1. Summary of gradations between the species and subspecies of *Lejopyge* from Sweden. The arrows indicate the presence of gradational characteristics, which include the over-all shape of the cephalon and pygidium, the degree of effacement, the width of the pygidial axis, the presence or absence of cephalic and pygidial spines, the length of spines, and the degree of cephalic scrobiculation.

Öpik (1967, p. 93) diagnosed *L. cos* as follows:

Lejopyge cos sp. nov. is distinguished by well developed posterior section of the cephalic axial furrows and rather distinct but relatively small basal lobes, short pygidial marginal spines, and two median nodes on the pygidial axial lobe; the additional node is placed on the anterior axial annulation.

Öpik's differential diagnosis of *L. cos* is as follows:

The marginal pygidial spines of *L. cos* are shared by *Lejopyge laevigata armata* (Linnarsson) but *armata* has only one node, on the second axial annulation; furthermore, the cephalic spines of *armata* are long (short in *cos*, as observed on specimens not illustrated).

The specimens figured by Westergård (1946, pl. 13, figs. 28, 29, 30, 31) as *L. l. armata* (Linnarsson) fit the diagnosis of *L. cos* perfectly. (The anterior of the two nodes cannot be seen in Westergård's figures.) The pygidia of *armata* (Westergård

1946, pl. 13, figs. 30, 31; Pl. 62, figs. 15, 16) have nodes on both the first and second pygidial axial segments in identical positions to the two nodes illustrated on *L. cos* by Öpik (1967, fig. 20). Close examination of the holotype pygidium of *L. cos* reveals the presence of a faint, but distinct, third node placed at about the centre of the third axial segment (Pl. 62, fig. 18). A third node in a similar position is also present on *L. laevigata*, *L. l. armata*, and on pygidia associated with the holotype cephalon of *L. l. perrugata* and *L. l. rugifera* and the unnamed subspecies of *L. calva* of Robison (1964a). Palmer (1968, p. 26) noted that *Lejopyge* has 'the posterior axial node on the axial lobe and not at its terminus, comparable to the position in *Ptychagnostus*'. The presence or absence of pygidial nodes and spines on the various species of *Lejopyge* is shown in Table 1. Not all pygidia possess a third node; where it is present it is usually small and faint and is not always visible in the photographs. However, in some specimens the node is reasonably prominent (e.g. Pl. 62, figs. 7, 8; Pl. 63, figs. 3, 9). At least one pygidium of *L. laevigata* (Westergård 1946, pl. 13, fig. 23; Pl. 62, fig. 7) has an anterior axial node as do some of the pygidia associated with the holotype cephalon of *L. l. perrugata*. In most pygidia not possessing a definite anterior axial node there is a slight general swelling in the expected position of the node. Thus the presence or absence of the first or third nodes cannot be used to differentiate *L. cos*, *L. laevigata*, and *L. l. armata*. The pygidium of *Ptychagnostus elegans laevisimus* (Westergård 1946, pl. 10, fig. 22; Pl. 63, fig. 13), the supposed ancestor of *L. laevigata*, shows no sign of either a first or a third pygidial node.

L. cos is also similar to *L. l. armata* in its pygidial spine characteristics. In this discussion of spine characters the line diagram of Öpik (1967, fig. 20) is referred to rather than his photograph of the holotype of *L. cos* (Öpik 1967, pl. 57, fig. 5; Pl. 62, fig. 18), because the border is poorly preserved on the holotype and Öpik had access to other unfigured pygidia of *L. cos*.

Öpik (1961a, p. 87; 1967, p. 93) maintained that *L. l. armata* has long cephalic and pygidial postero-lateral spines. However, Westergård (1946, pl. 13, figs. 28–36) allows great variations in the length of these spines—they vary from quite small to very long. Westergård (1946, p. 89) also notes, when discussing *armata* that:

Forms with shorter spines and more or less distinctly furrowed cheeks connect this long-spined and smooth form on the one hand with the typical *laevigata* and on the other hand with the subspecies *perrugata*.

This is borne out by a cephalon with short spines (Pl. 62, fig. 14) which occurs on the same slab as the pygidia figured as *L. l. armata* in Westergård (1946, pl. 13, figs. 30, 31) (see also Pl. 62, figs. 15, 16). Further, a cephalon figured as *L. laevigata* (Westergård 1946, pl. 13, fig. 24; Pl. 62, fig. 2) has short cephalic spines. The pygidia of *L. l. armata* (Westergård 1946, pl. 13, figs. 30, 31; Pl. 62, figs. 15, 16) have quite small spines which in fact are smaller than those of *L. cos* (Öpik 1967, p. 93, fig. 20). Thus, as far as cephalic and pygidial spines and pygidial nodes are concerned, *L. cos* and *L. l. armata* are indistinguishable. The over-all shape of the holotype pygidium of *L. cos* (Pl. 62, fig. 18) is similar to the shape of many of the pygidia of *L. laevigata* and *L. l. armata* figured by Westergård (1946). Unfortunately, the only cephalon of *L. cos* figured by Öpik (1967, pl. 57, fig. 6) (see also Pl. 62, fig. 17) is a poorly preserved collapsed specimen in which the border has not been preserved. Öpik's diagnosis of *L. cos* notes the well-developed posterior section of the cephalic axial furrows and the small

TABLE 1. Pygidial characteristics of the species and subspecies of *Lejopyge*.

Designated name or association	Figuring herein	Figuring in previous works	Spine characteristics	Axial nodes			Other remarks
				1	2	3	
<i>Lejopyge laevigata</i>	Pl. 62, fig. 7	Westergård (1946, pl. 13, fig. 23)	Absent	?	P	P	5 or 6 pairs of muscle scars. Associated with Dalman's syntype
<i>L. laevigata</i>	Pl. 62, fig. 4	Westergård (1946, pl. 13, fig. 26)	Absent	A	P	A	At least four pairs of muscle scars
<i>L. laevigata</i>	Pl. 62, fig. 10	Westergård (1946, pl. 13, fig. 25)	Very small	?	P	P	
<i>L. laevigata</i>	Pl. 62, fig. 8	Unfigured pygidium on same slab as cephalon figured in Westergård (1946, pl. 13, fig. 24)	Absent	P	P	P	Faint trace of post- axial median furrow
<i>L. laevigata</i>	Pl. 62, fig. 6	Unfigured pygidium on same slab as above specimen	Minute	A	P	P	Faint trace of post- axial median furrow
<i>L. laevigata</i>	Pl. 62, fig. 9	Westergård (1946, pl. 13, fig. 20)	Absent	A	P	P	
<i>L. laevigata</i>	Pl. 62, fig. 5	Unfigured specimen on same slab as above specimen	Absent	P	P	P	Trace of post-axial median furrow
<i>L. laevigata</i>	Pl. 62, fig. 1	Westergård (1946, pl. 16, fig. 9)	Absent	A	P	?	Complete specimen
<i>L. l. armata</i>	Pl. 62, fig. 15	Westergård (1946, pl. 13, fig. 30)	Very small	P	P	?	
<i>L. l. armata</i>	Pl. 62, fig. 16	Westergård (1946, pl. 13, fig. 31)	Very small	P	P	P	
Pygidium associated with holotype cephalon of <i>L. l. perrugata</i>	Pl. 63, fig. 3	Unfigured	Present	A	P	A	Broad low ridge posterior to node 2. Spines broken— length indeterminate
Largest pygidium associated with holotype cephalon of <i>L. l. perrugata</i>	Pl. 63, fig. 2	Unfigured	Present	?	P	P	Very large spine base
Pygidium associated with holotype cephalon of <i>L. l. perrugata</i>	Pl. 62, fig. 13	Unfigured	Large spines	P	P	P	
Pygidium associated with holotype cephalon of <i>L. l. perrugata</i>	Pl. 62, fig. 12	Unfigured	Present	P	P	P	
Pygidium associated with holotype cephalon of <i>L. l. rugifera</i>	Pl. 63, fig. 4	Unfigured	Absent	A	P	P	
Holotype pygidium of <i>L. cos</i>	Pl. 62, fig. 18	Öpik (1967, pl. 57, fig. 5)	Present	P	P	P	
<i>L. calva</i>	Unfigured	Robison (1964, pl. 83, fig. 3)	Absent	A	P	A	Strikingly effaced in both cephalon and pygidium
U.S.G.S. Collection 2523-CO (unnamed subspecies of <i>L. calva</i> , see Robison 1964a, p. 522)	Pl. 63, fig. 9	Unfigured	Absent	?	P	P	Wide border. Not all pygidia on this specimen have the third node
<i>Lejopyge</i> sp. (probably <i>L. calva</i>) from coquina, Patterson Pass, Snake Range, Nevada	Pl. 63, fig. 8	Unfigured	Absent	A	P	A	All pygidia in these specimens are strikingly effaced
<i>Ptychagnostus elegans laevissimus</i>	Pl. 63, fig. 13	Westergård (1946, pl. 10, fig. 22)	Absent	A	P	A	Wide axis

A = absent. P = present. ? = indeterminate.

but distinct basal lobes. However, the basal lobes of all species of *Lejopyge* are small. The rear part of the cephalic axial furrows of almost all the specimens of *L. laevigata* and its subspecies figured in Westergård (1946) and herein also have well-developed posterior axial furrows.

The facts noted above indicate that *L. cos* is a junior synonym of *L. l. armata*. Another point is that the pygidia of *L. l. armata*, as illustrated by Öpik (1961a, pl. 22, figs. 2, 3, 4) presumably have no node on the anterior axial annulation. Whether this is so or not cannot be clearly determined from the illustrations given by Öpik. If, in fact, there is no anterior node on the Queensland middle Cambrian and Passage Zone forms, then this may indicate a difference due to geographical variation. A further point of difference between the Swedish specimens of *L. l. armata* and those from Queensland illustrated by Öpik (1961a, pl. 22, figs. 2-4) is that in the Queensland forms the pygidial spines are posterior to those figured by Westergård (1946).

LEJOPYGE AND THE MIDDLE-UPPER CAMBRIAN BOUNDARY

Scandinavia

Within the Acado-Baltic province (type province of the Cambrian System) in both the Oslo region and adjacent parts of Sweden, the Cambrian occurs as very markedly condensed platform sequences. Although sections of these seemingly shallow-water deposits contain breaks, the painstaking collection and documentation of the fossils, mainly trilobites, has allowed a reliable and very fine zonation of the System, especially for the middle and upper Cambrian. Westergård (1922; 1946, p. 19; 1947, pp. 20-21) has shown that the most complete sections for the middle and upper Cambrian in Sweden are in Scania. However, even there breaks of varying magnitude are evident.

In Scandinavia the middle Cambrian-upper Cambrian boundary is drawn at the top of the *Lejopyge laevigata* Zone (see Tables 2 and 3). However, when discussing the biostratigraphy of the Swedish middle Cambrian, Westergård (1946, p. 7) pointed out that 'The boundary is not very well defined, the zone of *Lejopyge laevigata* merging into that of *Agnostus pisiformis*'. There are several reasons why this appears to be so:

1. In contrast to the rich and varied fauna of the *L. laevigata* Zone, only eight trilobite species or subspecies (even one of these questionably) are known in the *A. pisiformis* Zone in Sweden; three in Norway, where *Olenus alpha* Henningsmoen constitutes a further species. However, the rare *O. alpha* is unknown outside of the Ringsaker area (Henningsmoen 1957; 1958).

2. *A. pisiformis* (Linnaeus) is the only common trilobite in the *A. pisiformis* Zone, all other species being generally rare or absent in collections from most localities where the zone is recognized. The fossils which occur in black bituminous shales (alum shales) and dark bituminous limestone (stinkstone) were probably specialized planktonic forms that were able to avoid the poisonous bottom habitat (Bergström *et al.* 1972).

3. Of the trilobites found in the *A. pisiformis* Zone only *A. pisiformis* ranges down into the *L. laevigata* Zone (Table 2). Originally Westergård (1947, p. 22) showed

TABLE 2. Trilobite zonation for the late middle Cambrian–early upper Cambrian of Sweden. The ranges of the majority of Scandinavian trilobites mentioned in the text are presented to facilitate discussion. The thicknesses given for the various divisions are taken from Westergård (1944a, p. 29). The unbracketed figures are for the Andrarum No. 1 borehole; those bracketed are for the Sodra Sandby borehole about 40 km west of Andrarum, Scania. Note that the thickness for the *L. laevigata* Zone includes the unfossiliferous interval 1.0 m (3.0) immediately below the designated *A. pisiformis* Zone.

MIDDLE CAMBRIAN		UPPER CAMBRIAN				
				SWEDISH ZONES		
		Agnostus pisiformis		Olenus		
		4.5m(6.1)		11.4m(12.7)		
				Sub-zones with Olenus spp.		
				a b c d e f		
				1.5m(2.5) 0.5m(1.2) 0.6m		
		Upper part				
		Lower part				
		3.0m(8.1)				
		0.9m(1.2)				
		12m(3.5)				
		x	x			Acrocephalites stenometopus
		x	x			Acrocephalites stenometopus agnostorum
		x	x			Acrocephalites stenometopus olenorum
		x	x			Agnostus pisiformis
		x	x			Agnostus pisiformis subsulcatus
		x	x			Clavagnostus sulcatus
	x	x	x			Diplagnostus planicauda vestgothicus
		x	x			Drepanura eremita
				x	x	Glyptagnostus reticulatus
				x	x	Glyptagnostus reticulatus nodulosus
				x	x	Homagnostus obesus
					x	Hypagnostus sulcifer
						Lejopyge laevigata
						Lejopyge laevigata armata
						Oidagnostus trispinifer
						Olenus alpha
						Peronopsis insignis
						Phalacroma glandiforme
						Phalagnostus bituberculatus
						Proceratopyge conifrons
						Proceratopyge nathorsti
						Ptychagnostus (Goniagnostus) spiniger
						Ptychagnostus (Ptychagnostus) aculeatus
						Schmalenseeia amphioneura
						Solenopleura brachymetopa

Acrocephalites stenometopus (Angelin) in the *Agnostus pisiformis* and *Olenus* Zones, but he later (1948) referred forms from each of these zones to the subspecies *A. stenometopus agnostorum* and *A. s. olenorum* respectively (Table 2). Moreover, he regarded the middle Cambrian *A. stenometopus* and its two upper Cambrian subspecies as constituting an evolutionary series which spanned the middle–upper Cambrian boundary. Thus in Scandinavia and elsewhere, rocks with *L. laevigata* signify the middle Cambrian.

4. Where unfossiliferous intervals occur between rocks containing the *L. laevigata* and *Agnostus pisiformis* faunas, there must be an interval of uncertainty concerning the zonal and series boundaries. In practice, the boundary has been drawn either immediately above the barren interval (Westergård 1944*a, b*) or immediately below it (Westergård 1922, p. 18).

Should a convenient reference section for the middle–upper Cambrian boundary be required, the section described by Westergård (1922, fig. 33, pp. 67–68) from Ödegården, Falbygden district in Västergötland would be suitable, for at that locality the *L. laevigata* and *A. pisiformis* Zones are in contact and the ranges of the two nominate zonal species overlap. This unbroken section provides an unambiguous solution to the boundary problem.

The Cambrian world exclusive of Scandinavia

Australia. Since *Lejopyge cos* Öpik is a synonym of *L. laevigata armata* (Linnarsson), it is evident that *L. l. armata* ranges as high as the Mindyallan Zone of *Cyclagnostus quasivespa* (see Öpik 1967, Table 4, p. 41). Providing the upper limits of the ranges of this subspecies are the same in Queensland and Sweden then part of the *C. quasivespa* Zone and the top part of the Swedish *L. laevigata* Zone are correlatives (Table 3).

The described specimens of *L. cos* came from the Mungerebar Limestone at locality G 131 in the Zone of *C. quasivespa*. In the Mungerebar–Mindyalla area dips are low and outcrops are small and discontinuous so that Öpik's stratigraphic succession was pieced together on faunal evidence rather than on superposition. This has led to uncertainties, for example, Öpik (1967, vol. 2, p. 9) commented that the collection from locality G 131 was 'apparently below G 130' which among other species contained *Blackwelderia sabulosa* Öpik. As indicated on the collection locality map (Öpik 1967, fig. 3, p. 12), the G 131 site is not far removed from the lower boundary of the zonal limits. An analysis of faunal lists from collecting sites within the *C. quasivespa* Zone suggests a clear separation of the G 131 fauna (and its presumed equivalent the G 10 fauna, see Öpik 1967, vol. 2, p. 6) from those containing *B. sabulosa* (G 124–G 127; G 130), which as he suggested are presumably younger. Thus for the Australian region it is advocated that the middle–upper Cambrian boundary be drawn within the *C. quasivespa* Zone between the *L. cos* (= *L. l. armata*) and *B. sabulosa* faunas (Table 3). In passing, we note that in Australia *Blackwelderia* was already present in the late middle Cambrian for at locality G 119, *B. cf. sabulosa* is found in the zone of *E. eretes*. Moreover, *Blackwelderia* succeeds *Damesella* in Australia as in China. In Australia *Damesella* first appears in the *D. torosa*–*A. janitrix* Zone and *D. torosa* itself ranges into the *E. eretes* Zone (Öpik 1967, p. 307) where *Blackwelderia* is present.

TABLE 3. Correlation chart of late middle and early upper Cambrian trilobite faunas of Scandinavia and other areas discussed in the text. It should be noted that the top and bottom lines of the correlation chart have no temporal significance, e.g. it does not indicate that the top of the North American *Aphelaspis* Zone corresponds to the top of the *Glyptagnostus reticulatus* Zone from Australia or that the base of the North American *Bolaspideella* Zone is equivalent to the base of the Swedish *Solenopleura brachymetopa* Zone. Chu (1959) uses the term *Damesella paronai* Zone rather than the *D. blackwelderi* Zone.

CAMBRIAN	ENGLAND	SWEDEN	AUSTRALIA	NORTH AMERICA	CHINA	SIBERIAN PLATFORM	NORTH-WEST SIBERIA
UPPER	OUTWOODS SHALES	Olenus	DAMEAN STAGE Glyptagnostus reticulatus	Aphelaspis		STAGE Glyptagnostus reticulatus	
		Agnostus pisiformis	STAGE Glyptagnostus stolidotus	Crepecephalus	Drepanura premesnili	STAGE Glyptagnostus stolidotus	Pedinocephalina-Toxotis(?)
CAMBRIAN	MANCETTER GRITS AND SHALES		MINDYLLAN STAGE Cyclagnostus quasivespa	DRESBACHIAN STAGE Cedaria	KUSHAN FORMATION Blackwelderia sinensis	AGNOSTUS pisiformis - Homagnostus fecundus	SAAMINSKI SUBSTAGE Acrocephalota granulosa - Koldinella prolata
		Lejopyge laevigata	Erediaspis eretes			Damesella blackwelderi	Lejopyge laevigata armata - Lomuscaspis alta
MIDDLE		Solenopleura brachymetopa	Proampyx agra OR laevigata II Psychagnostus cassis OR laevigata I	Bolaspideella			SAAMINSKI HORIZON Agraucos punctatus

Notes: 1 and 2. The age of the basal part of the Mancetter Grits and Shales is uncertain and may range within the limits shown. 3 and 4. The relative positions of two important fossils in the Merevale No. 3 Borehole.

Notes 5 and 6. The lower boundary of the *Malaspis spinosa-Oidagnostus trispinifer* Zone is shown extending to position 5, well into the *Solenopleura brachymetopa* Zone. Table 4 which is based mainly on Datsenko *et al.* (1968, 'Atlas', pp. 28-31) shows that the ranges of *Phalacroma glandiforme* and *Oidagnostus trispinifer* overlap. Consequently, if it is conceded that *P. glandiforme* ranges into the Swedish *L. laevigata* Zone, then this boundary will need to be shifted to approximately position 6.



TABLE 3. Correlation chart of late middle and early upper Cambrian trilobite faunas of Scandinavia and other areas discussed in the text. It should be noted that the top and bottom lines of the correlation chart have no temporal significance, e.g. it does not indicate that the top of the North American *Aphelaspis* Zone corresponds to the top of the *Glyptagnostus reticulatus* Zone from Australia or that the base of the North American *Bolaspidea* Zone is equivalent to the base of the Swedish *Solenopleura brachymetopa* Zone. Chu (1959) uses the term *Damesella paronai* Zone rather than the *D. blackwelderi* Zone.

	ENGLAND	SWEDEN	AUSTRALIA	NORTH AMERICA	CHINA	SIBERIAN PLATFORM	NORTH-WEST SIBERIA
UPPER CAMBRIAN	OUTWOODS SHALES	Olenus	IDAMEAN STAGE	STAGE	Aphelaspis	STAGE	Glyptagnostus reticulatus
		Agnostus pisiformis					
CAMBRIAN GRITS AND SHALES	Lejopyge laevigata	Lejopyge laevigata	MINDYALLAN STAGE	DRESBACHIAN	Cedaria	STAGE	Agnostus pisiformis - Homagnostus fecundus
MIDDLE CAMBRIAN	Mancetter Grits and Shales (3) (4)	Damesella torosa - Ascionepea janitrix	Gamesella blackwelderi	TUORIAN	Acrocephaleta granulosa - Koldaniella proluxa		
						Mancetter Grits and Shales (5) (6)	Proximpyx agra OR laevigata II
Mancetter Grits and Shales (7) (8)	Ptychagnostus cassis OR laevigata I	Ptychagnostus cassis OR laevigata I	Agraulos punctatus				

Notes: 1 and 2. The age of the basal part of the Mancetter Grits and Shales is uncertain and may range within the limits shown. 3 and 4. The relative positions of two important fossils in the Merevale No. 3 Borehole.

Notes 5 and 6. The lower boundary of the *Maiaspis spinosa*-*Oidalgagnostus trispinifer* Zone is shown extending to position 5, well into the *Solenopleura brachymetopa* Zone. Table 4 which is based mainly on Datsenko *et al.* (1968, 'Atlas', pp. 28-31) shows that the ranges of *Phalacroma glandiforme* and *Oidalgagnostus trispinifer* overlap. Consequently, if it is conceded that *P. glandiforme* ranges into the Swedish *L. laevigata* Zone, then this boundary will need to be shifted to approximately position 6.

The vast majority of all the other trilobites listed in Öpik's Table 4 are endemic species and so have little value for refined intercontinental correlations. However, a check of the non-endemic forms listed suggests that the correlation proposed above is correct. The following species of agnostids listed by Öpik deserve comment (reference to Tables 2 and 3 will assist the reader):

1. In Sweden *Ptychagnostus (Goniagnostus) spiniger* (Westergård) occurs in the 'Zone of *Lejopyge laevigata*, basal layer' (Westergård 1946, p. 82). Öpik (1967, p. 90) reported this species from limestone in the Northern Territory (locality T 87) and from the Steamboat Sandstone in Queensland (localities G 106 and D 96). In the discussion of the Australian material Öpik (1967, p. 90) stated that *P. (G.) spiniger* occurs 'in the upper part of the *L. laevigata* II and in the *laevigata* III Zones'. Now the *L. laevigata* III Zone is shown as the uppermost middle Cambrian Zone in the biostratigraphic chart given by Öpik (1961a, fig. 15, p. 34). However, from the Devoncourt Limestone (locality D 18, which is a direct correlative of, or at the most one zone older than the T 87 fauna cited above) and the older Roaring Siltstone (locality D 7/15) in Queensland, Öpik (1961a, p. 44) reported *Ptychagnostus (Ptychagnostus) aculeatus* (Angelin), a species which in Sweden is confined to the *Solenopleura brachymetopa* Zone. Thus, the positioning of the D 18 fauna on Öpik's chart (Öpik 1961a, fig. 15, p. 34) appears to be too high in terms of the Swedish zonal scale and in the writers' opinion the Australian *L. laevigata* II Zone is not younger than the upper half of the Swedish *S. brachymetopa* Zone. The occurrence of the Swedish *Diplagnostus planicauda vestgothicus* (Wallerius) in the D 18 fauna also tends to support the correlation of the Australian *L. laevigata* II Zone with the Zone of *S. brachymetopa* although in Sweden this form also occurs in the overlying *L. laevigata* Zone. Thus it appears likely that the *L. laevigata* III Zone will correlate approximately with the basal part of the Swedish Zone of *L. laevigata*. In terms of the Swedish Scale we suggest that *P. (G.) spiniger* in Australia spans the boundary separating the *S. brachymetopa*-*L. laevigata* Zones.

2. Öpik (1967) showed that *Oidalagnostus trispinifer* Westergård ranged from the late middle Cambrian *L. laevigata* III Zone (localities G 121 and G 133) to the Zone of *C. quasivespa* (locality G 131) where it is associated with *L. cos*. Further, Öpik (1967, p. 134) stated that *O. trispinifer* occurs in the superjacent zone of *Glyptagnostus stolidotus* in Tasmania. However, the only species of *Oidalagnostus* from Tasmania known to the writers is indeterminate. Its age is probably the *Erediaspis eretes* Zone or the *C. quasivespa* Zone.

In Sweden the very rare *O. trispinifer* has been found only in the upper part of the *L. laevigata* Zone (Westergård 1946, p. 67). (Dr. Lars Karis, Geological Survey of Sweden (pers. comm.), has found *O. trispinifer* in a limestone concretion containing faunal elements of the Zone of *S. brachymetopa* in the Tåsjö area, central Swedish Caledonides. Thus the stratigraphic range of this species is more extensive than that shown on Table 2. Consequently, the lower boundary of the Siberian Zone of *Maiaspis spinosa*-*O. trispinifer* can now be confidently drawn at position 5 on Table 3.) Thus it seems likely that the lower portions of the *C. quasivespa* Zone and the top part of the Swedish *L. laevigata* Zone are correlatives and that the species may in fact cover the full range of the Swedish *L. laevigata* Zone. This latter suggestion

TABLE 4. Stratigraphic distribution of trilobites important for the correlation of the north-west Siberian middle and upper Cambrian rocks. The relative sizes of the zones and the ranges of the fossils were calculated from Datsenko *et al.* (1968, 'Atlas', pp. 28-31) and Rosova (1968).

ZONES TRILOBITES	<i>Agraulos punctatus</i>	<i>Maiaspis spinosa</i> — <i>Oidagnostus trispinifer</i>	<i>Acrocephalella granulosa</i> — <i>Koldiniella proluxa</i>	<i>Pedinocephalina</i> — <i>Toxotis</i> (?)
<i>Phalacroma glandiforme</i> <i>Maiaspis spinosa</i> <i>Oidagnostus trispinifer</i> "Homagnostus fecundus" <i>Grönwallia decora</i> <i>Koldiniella convexa</i> <i>Nganasella nganasanensis</i> <i>Acidaspidella limita</i> <i>Pseudagnostus nganasanicus</i> "Peronopsis insignis" "Clavagnostus sulcatus"				
			x	
				x
			-	
			-	
			x x	—
			-	
				x

is supported by the common occurrence of *O. trispinifer* in north-western Siberia in the middle Cambrian Mayanian Stage where according to Datsenko *et al.* (1968, in 'Atlas of stratigraphic schemes', pp. 28-29) it is found in all but the basal part of the Zone of *Maiaspis spinosa*-*Oidagnostus trispinifer* which, in our opinion (see below), marks the top of the middle Cambrian (Table 4).

3. An agnostid cephalon from the Mungerebar Limestone (locality G 119, Zone of *E. eretes*) figured (Öpik 1967, pl. 58, fig. 1) as *Aagnostus?* sp. aff. *Aagnostus pisiformis subsulcatus* Westergård, may belong in our opinion to Westergård's subspecies which was described by him from the *Paradoxides forchammeri* beds, although on his range chart (Westergård 1946, p. 102), he indicated that the species occurred only in the *L. laevigata* Zone. Apart from minor taxonomic differences it would seem that the uncertainty of Öpik's assignment was partly influenced by the belief that the *E. eretes* Zone was younger than the *L. laevigata* Zone of Sweden.

4. According to Öpik (1967, pp. 131-132) the *Proagnostus?* sp. from Woodstock, Alabama, U.S.A. (see Palmer 1962), is *Connagnostus venerabilis* Öpik, a species which in Australia is confined to the *Glyptagnostus stolidotus* Zone. It is one of the few new species of Australian agnostids described by Öpik common to both continents. Of even greater significance is its occurrence in Alabama, in the Conasauga Formation, in association with *G. stolidotus* Öpik (Palmer 1962, fig. 4) the nominate zone fossil for the uppermost zone of the Australian Mindyallan Stage. Thus the intercontinental

correlation of the *G. stolidotus* Zone with the lower levels of the *Crepicephalus* Zone in North America and probably an undefined part of the subjacent *Cedaria* Zone seems assured (Table 3). Further, in both Australia and North America *G. stolidotus* is succeeded by *Glyptagnostus reticulatus* (Angelin) (Öpik 1961*b*, 1963; Palmer 1962, Table I, p. 7). *G. reticulatus* is also present in Sweden where it occurs in the two oldest subzones of the *Olenus* Zone and its subspecies *G. r. nodulosus* Westergård passes into the overlying subzone.

Therefore it seems that providing the lower part of the *C. quasivespa* Zone marks the top of the Swedish *L. laevigata* Zone as indicated above, then the upper part of the *C. quasivespa* Zone (from the base of the *B. sabulosa* fauna) together with the overlying *G. stolidotus* Zone must equate with the Scandinavian *A. pisiformis* Zone. Thus in Australia the middle-upper Cambrian boundary would occur within the Mindyallan Stage and within the *C. quasivespa* Zone as shown in Table 3.

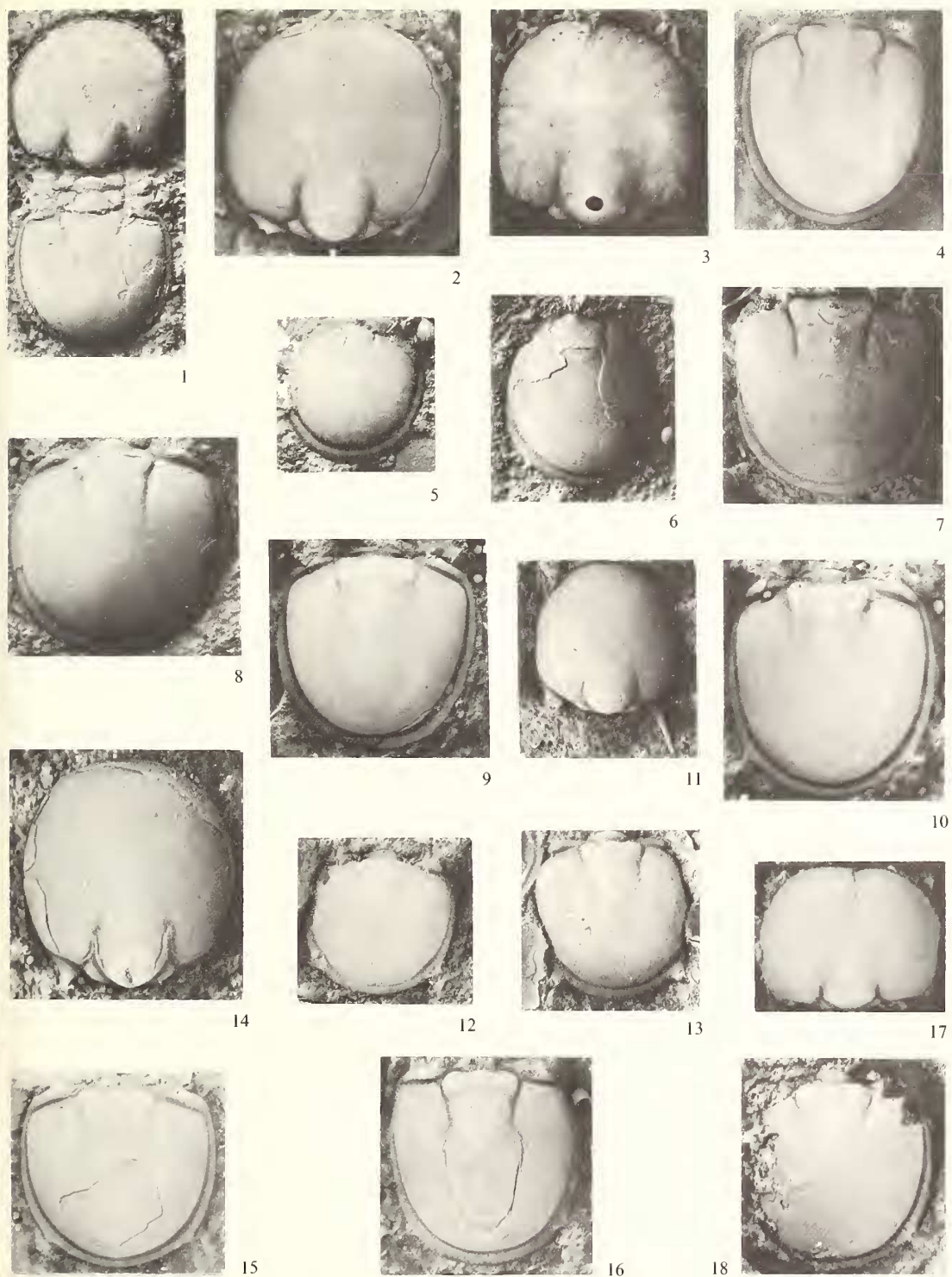
Great Britain. Until recently the *L. laevigata* and *A. pisiformis* Zones were unknown with certainty in Britain but they have now been positively identified from fossils obtained from the Merevale No. 3 Borehole, Warwickshire (Rushton *in* Taylor and Rushton 1972; Cowie *et al.* 1972). However, *L. laevigata* has not yet been found in British rocks. The *L. laevigata* Zone is present within the Mancetter Grits and Shales. The oldest identifiable fossil within this formation is the bradoriid crustacean *Svealuta primordialis* (Linnarsson). It was found one-third of the way through the formation but fragments assigned to this species occur almost to its base. In Sweden the species occurs in the *L. laevigata* Zone (Westergård 1944*a*, p. 33) and it is 'abundant in the Zone with *Solenopleura brachymetopa*' (Öpik 1961*a*, p. 175). Hence it seems

EXPLANATION OF PLATE 62

All figures are rubber casts whitened with magnesium oxide prior to photography. All figures are untouched.

Figs. 1-10. *Lejopyge laevigata* (Dalman). 1, complete specimen (Westergård 1946, pl. 16, fig. 9) from Ullavi (boulder), Närke, $\times 7.3$. 2, cephalon (Westergård 1946, pl. 13, fig. 24) from Djupadalen, Västergötland, $\times 8.4$. 3, cephalon showing scrobiculation (Westergård 1946, pl. 13, fig. 22) from Hönsäter, Kinnekulle, Västergötland, $\times 11.2$ (the black hole is a hole in the cast). 4, pygidium (Westergård 1946, pl. 13, fig. 26) from Gudhem, Västergötland, $\times 8$. 5, small pygidium showing post-axial median furrow (associated with specimen figured Pl. 62, fig. 9), Andrarum, Scania, $\times 12.4$. 6, minutely spinose pygidium (associated with cephalon figured Pl. 62, fig. 2), Djupadalen, Västergötland, $\times 10$. 7, pygidium (Westergård 1946, pl. 13, fig. 23) from Hönsäter, Kinnekulle, Västergötland, $\times 8$. Note the very faint third pygidial node and the several pairs of muscle scars on the third pygidial lobe. 8, pygidium (associated with cephalon figured Pl. 62, fig. 2), Djupadalen, Västergötland, $\times 10$. 9, pygidium (Westergård 1946, pl. 13, fig. 20) from Andrarum, Scania, $\times 9.7$. 10, pygidium (Westergård 1946, pl. 13, fig. 25) from Djupadalen, Västergötland, $\times 8$.

Figs. 11-18. *Lejopyge laevigata armata* (Linnarsson). Figs. 11, 12, 13 are of specimens associated with the cephalon (Westergård 1946, pl. 14, fig. 2) figured herein (Pl. 63, fig. 1) as the holotype of *Lejopyge laevigata perrugata* from Karlfors, Billingen, Västergötland. 11, cephalon with long spines, $\times 8.4$. 12, pygidium with long spines, $\times 7.9$. 13, small pygidium, $\times 10$. 14, spinose cephalon associated with pygidia of *Lejopyge laevigata armata* (see Pl. 62, figs. 15, 16) from Gudhem, Västergötland, $\times 13$. 15, pygidium with small spines (Westergård 1946, pl. 13, fig. 30), $\times 7.6$. 16, pygidium with small spines (Westergård 1946, pl. 13, fig. 31), $\times 7.5$. 17, crushed cephalon (Öpik 1967, pl. 57, fig. 6 as *Lejopyge cos*) from Mungerebar Limestone, Queensland at Lat. $22^{\circ} 15.5' S.$, Long. $139^{\circ} 01' E.$, $\times 13.5$. 18, pygidium figured (Öpik 1967, pl. 57, fig. 5) as holotype of *Lejopyge cos*, Mungerebar Limestone, Queensland, at Lat. $22^{\circ} 15.5' S.$, Long. $139^{\circ} 01' E.$, $\times 9.4$.



likely that the lower third of the Mancetter Grits and Shales could conceivably incorporate part of the *S. brachymetopa* Zone, rather than all of it belonging to the *L. laevigata* Zone as suggested by Rushton. Such an uncertainty is expressed in Table 3. Irrespective of its age, the basal part of the formation is a conglomerate (see also Illing 1916, p. 395; Stubblefield 1956, p. 31) which may reflect an erosional event comparable with that of the Exporrecta conglomerate of Sweden. The youngest fossil which can be assigned confidently to the *L. laevigata* Zone is *Hypagnostus sulcifer* (Wallerius), found near the top of the formation. Westergård (1946, p. 52) reports this species only from the upper part of the Swedish *L. laevigata* Zone.

The *A. pisiformis* Zone is contained with certainty in the lower part of the overlying Outwoods Shales. *A. pisiformis* and *Schmalenseia* cf. *amphionura* occur together at or near the base of the zone, a 10-m interval below this level remaining unassigned due to lack of diagnostic fossils.

An important find about three-fifths of the way through the Mancetter Grits and Shales was *Ptychagnostus* (*Goniagnostus*) *fumicola* Öpik (Rushton in Taylor and Rushton 1972, p. 9). However, on the bore log record (ibid., pl. 4) the identification appears to be less certain for there it is given as *Ptychagnostus* cf. *fumicola*. Through the kind efforts of Dr. A. Rushton we have examined latex casts of this material and believe that the assignment of *P. (G.) fumicola* Öpik is correct. Now in the Mungerebar area in Queensland, *P. (G.) fumicola* occurs with *Oidagnostus trispinifer* in rocks (locality G 121) referred by Öpik (1967, p. 91) to the *L. laevigata* III Zone. It is also found in the succeeding zone with *Damesella torosa* and *Ascionepe janitrix* which Öpik called the middle-upper Cambrian zone of passage. However, as pointed out above, *O. trispinifer* in Queensland is known to range upwards into the *C. quasivespa*

EXPLANATION OF PLATE 63

All figures are photographs of rubber casts, except figs. 7 and 8 which are of the actual specimens. All were whitened with magnesium oxide prior to photography. All figures are untouched. Catalogue numbers are those of the palaeontology collections, South Australian Museum, Adelaide, South Australia.

Fig. 1. Holotype cephalon of *Lejopyge laevigata perrugata* (Westergård 1946, pl. 14, fig. 2) from Karlfors, Billingen, Västergötland, $\times 9$.

Figs. 2, 3. Pygidia associated with the holotype cephalon of *Lejopyge laevigata perrugata*. 2, pygidium with very large spine base, $\times 10.8$. 3, pygidium with broad low ridge posterior to the second axial node, $\times 11$.

Figs. 4, 5. Pygidium and rugose cephalon associated with the holotype cephalon of *Lejopyge laevigata rugifera* from Sjögestad, Östergötland. 4, pygidium, $\times 7.7$. 5, cephalon, $\times 7.4$.

Fig. 6. Holotype cephalon of *Lejopyge laevigata rugifera* (Westergård 1946, pl. 14, fig. 3), $\times 8.4$.

Figs. 7, 8. *Lejopyge* sp. (probably *Lejopyge calva*) from coquina at Patterson Pass, Snake Range, East Nevada. 7, P. 14545, cephalon, $\times 8.8$. 8, P. 14546, pygidium, $\times 10.4$.

Fig. 9. Pygidium of unnamed subspecies of *Lejopyge calva* (see Robison 1964a, p. 522) from U.S. Geological Survey Collection 2523-CO, Schell Creek Range, Nevada, $\times 8.5$. Note the third pygidial node.

Fig. 10. *Lejopyge calva* Robison, holotype cephalon (Robison 1964a, pl. 83, fig. 1) from 1336 ft above base of the Marjum Formation, Wheeler Amphitheater, House Range, Western Utah, $\times 10.3$.

Fig. 11. *Lejopyge exilis* pygidium (Whitehouse 1936, pl. 9, fig. 12) from 8 miles north-east of Duchess, Queensland, $\times 7.1$.

Figs. 12, 13. *Ptychagnostus elegans laevissimus* Westergård, from Gislövshammer (boulder 18), Scania. 12, holotype cephalon (Westergård 1946, pl. 10, fig. 21), $\times 9.7$. 13, pygidium (Westergård 1946, pl. 10, fig. 22), $\times 8.1$.

Figs. 14, 15. *Drepamura eremita* Westergård, 14, cranidium (Westergård 1947, pl. 3, fig. 9), locality unknown, $\times 3.5$. 15, holotype pygidium (Westergård 1947, pl. 3, fig. 11) from Djupadalen, Västergötland, $\times 2$.



1



2



3



4



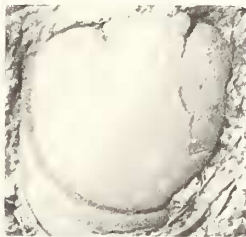
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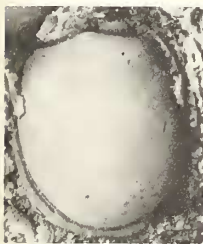
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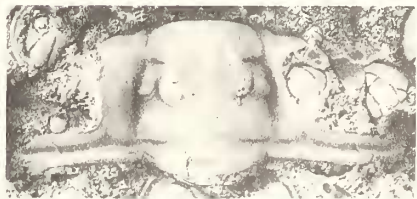
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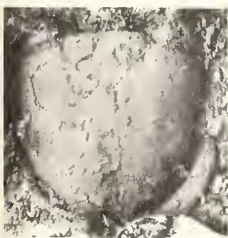
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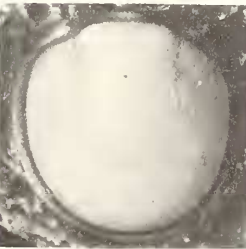
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13



15

Zone where, at locality G 131, it is associated with *L. cos* Öpik (= *L. l. armata*) and *Svealuta* cf. *primordialis*. The range of the British *P. (G.) fumicola* is unknown, being found only in one thin bed, just above the mid-point of the interval allotted by Rushton to the *L. laevigata* Zone. Unfortunately, without further fossil control on the upper and particularly the lower limits of the zone, the value of *P. (G.) fumicola* for refined intercontinental correlation remains untested. Nevertheless, as the species occurs well below the occurrence of *H. sulcifer*, which in Sweden seems to have the same range as *O. trispinifer*, it appears likely that *P. (G.) fumicola* may be confined to the interval represented by the central portion of the Swedish *L. laevigata* Zone.

North America. In North America *L. calva* Robison occurs in the uppermost subzone of the late middle Cambrian *Bolaspidella* Assemblage Zone. Lu (1960, p. 213) and Robison (1964*b*) independently proposed that the middle-upper Cambrian boundary in North America be placed at the top of the *Bolaspidella* Zone. In reaching his conclusion Robison (1964*b*) assumed that the range of *L. calva* was contained within the time interval occupied by the Swedish Zone of *L. laevigata*. However, Palmer (1968, p. 10) has shown that in Canada *L. calva* is associated with *Phalagnostus bituberculatus* (Angelin) and *Ptychagnostus (P.) aculeatus* (Angelin) both of which in Sweden are confined to the *S. brachymetopa* Zone (Table 2). Palmer (1968, p. 10) also reported *L. laevigata* from the Hillard Peak area in Alaska within a mile or so of the Canadian occurrence of *L. calva*. Unfortunately, both species are unknown in the same section in Alaska (or elsewhere), and thus all that can be said presently with any degree of certainty is that *L. calva*, based on the Canadian occurrence, covers only the lower part of the range of *L. laevigata*. Thus in North America the middle-upper Cambrian boundary may well lie within the *Cedaria* Zone rather than at its base as suggested by Robison (1964*b, c*). Using the generic range of trilobites, Palmer (1962, fig. 9) was the first to suggest that the Series boundary lay somewhere within the *Cedaria* Zone. This conclusion is in harmony with our views (Table 3), which, however, are based on more recent information at the species level. Indeed, it is the writers' view that correlations based on species have the best chances of being correct, for the accuracy of correlation using genera or higher taxa is of a much lower order and should be viewed as such. For example, of the many polymerid species listed by Öpik (1967, Table 4), only *Corynexochus plumula* Whitehouse and *Stephanocare richthofeni* Monke presently allow for intercontinental correlation. *Corynexochus* has in the past been regarded as a middle Cambrian genus. However, the anachronistic *C. plumula*, which succeeds *G. reticulatus* in all its known occurrences in Australia and elsewhere (Öpik 1963; Palmer 1968), is clearly upper Cambrian in age.

China. Recently, Kobayashi (1967, p. 476, and fig. 5, p. 477) has discussed and shown the areal distribution of three distinct Cambrian faunas in eastern Asia. Two of these, namely the Hwangho Fauna and the Chiangnan Fauna are of interest here. The Hwangho Fauna is a shallow-sea fauna which contains mainly endemic elements with rare cosmopolitan elements. In contrast, the Chiangnan Fauna is interpreted as a pelagic or offshore fauna preserved in mainly black carbonaceous shales; its facies is similar to the dark-coloured Scandinavian alumshale and stinkstone facies.

S. richthofeni, an important member of the Hwangho Fauna, provides a firm correlation of the Australian *C. quasivespa* Zone with part of the Kushan Formation

sensu stricto, of northern China. There *S. richthofeni* is confined to the *Blackwelderia paronai* Zone (elsewhere in the text and Table 3 the term *B. sinensis* Zone is used in preference to the term *B. paronai* Zone) and the lower part of the succeeding *Drepanura premesnili* Zone (Chu 1959). Sun (1948), on the basis of the occurrence of *D. eremita* Westergård in the Swedish *A. pisiformis* Zone, argued for an early upper Cambrian age for the Kushan Formation *sensu stricto*. Öpik (1967) assigned both *D. eremita* and *D. ketteleri* Monke (note *D. ketteleri* is confined apparently to the *D. premesnili* Zone) to *Palaeadotes* Öpik, which in Australia occurs in both the *C. quasivespa* and *G. stolidotus* Zones. *Palaeadotes* Öpik is, however, a synonym of *Bergeronites* Sun whose genotype is *Drepanura ketteleri* Monke (see Kuo 1965, p. 637). We have re-examined *D. eremita* and believe that although it is close to *Bergeronites* it should be reassigned to a new genus. For example, its anterior facial sutures are distinctly divergent and not convergent as in *Bergeronites* and its pygidium has a well-defined border (see Pl. 63, figs. 14, 15). Thus, less importance should be accorded this species for intercontinental correlation than has been in the past.

In contrast to the paucity of agnostids in the Hwangho Fauna, there is a relative abundance of cosmopolitan agnostids in the Chiangnan Fauna. This fauna occurs in a broad north-easterly trending belt of rocks across south-eastern China and embraces parts of South Korea. Within this belt, on the Hunan-Kueichow border in southern China, Egorova *et al.* (1963) have reported *Drepanura* in the Para-Kushan Fauna in association with *Proceratopyge conifrons* Wallerius, a species confined to the upper part of the Swedish *L. laevigata* Zone (Table 2). At another locality *Drepanura* was found with '*Glyptagnostus fossus*' Pokrovskaya (= *G. stolidotus* Öpik) and *G. reticulatus* (Kobayashi 1971, Table 13, p. 177). Hence, in terms of the Scandinavian scale, and providing the determinations of the fauna are correct (we have not seen Egorova *et al.* 1963), *Drepanura* (or Drepanurinae if the determinations are not precise) would range from the upper part of the *L. laevigata* Zone to at least the base of the *Olenus* Zone where *G. reticulatus* is present in its lower part. Note that in Australia Öpik (1961*b*, p. 430) reports that *G. stolidotus* and *G. reticulatus* 'overlap for a short interval (represented by a few feet of sediment only)'. This range for the Drepanurinae, therefore, is comparable to that cited above for Queensland. However, in northern China, Chu (1959) has shown that *Drepanura* and *Bergeronites* are presumably restricted to the *D. premesnili* Zone whereas *S. richthofeni* ranges downwards into the lower levels of the *B. sinensis* Zone. As *Bergeronites* aff. *dissidens* occurs in Queensland in the *C. quasivespa* Zone with *L. laevigata armata* [= *L. cos*] (Locality G131) and with *S. richthofeni* (Locality G153) it would seem that the *B. sinensis* and *C. quasivespa* Zones are correlatives either fully or at least in part and that the *D. premesnili* Zone must in turn be correlated with the Australian *G. stolidotus* Zone and the upper part of the Swedish *A. pisiformis* Zone (Table 3). This agrees with conclusions cited above. Likewise the *Stephanocare* Zone below the *Drepanura* Zone in South Korea will correlate to the *C. quasivespa* Zone as *S. richthofeni* is confined to the *Stephanocare* Zone in that region.

Within the Chiangnan faunal belt in China, Kobayashi (1967, pp. 459-461) has reported the occurrence of *Lejopyge* in the Yanglioukang limestone in west Chekiang and south Anhwei provinces. In west Chekiang *L. l. armata* occurs in the upper part of the formation (Kobayashi 1971, p. 176) and below *Glyptagnostus* beds above. In

south Anhwei *Lejopyge* occurs below rocks with *Drepanura*, *Blackwelderia*, and *Proceratopyge* and many other genera, but further pertinent details are unavailable to us. Kobayashi (1967, p. 501) also reports *Lejopyge* from the dark- and light-grey bedded limestones and shales of the Mēhuershan Series in the Eastern Tianshan. *Glyptagnostus* occurs in the 25-m thick basal member of the overlying Torsuqtagh Series.

In presenting a list of the middle and upper Cambrian trilobites from the Chiangnan faunal belt of central and south China, Kobayashi (1967, p. 462) reported *L. l. armata* in the middle Cambrian sequence of the Kueichow-Hunan border region. Its occurrence is listed together with the Swedish agnostids *Ptychagnostus aculeatus* (Angelin), *P. atavus* (Tullberg), and *Diplagnostus planicauda bilobatus* Kobayashi. We have been unable to check either the original locality data (presumably this is in Egorova *et al.* 1963) to see if further stratigraphic refinement is possible, or to check the fossil identifications. However, in the *Handbook of standard fossils of south China* (Chinese Academy of Science, 1964) some of the named species are figured but without accompanying locality and stratigraphic data. We believe the squashed specimen on plate 3, fig. 10 therein is correctly referred to *L. l. armata* although we have some reservations about the identity of their *P. atavus* (pl. 2, figs. 8, 9). The material figured as *P. aculeatus* (pl. 2, figs. 10, 11) is not Chinese but Swedish material figured by Westergård (1946, pl. 12, figs. 9, 8). Judging the data presented by Kobayashi (1971, pp. 175-177) it seems likely that the listed *L. l. armata* is from the west Chekiang occurrence cited above and that it has been inadvertently placed in the list of material from the Kueichow-Hunan border. Until more concrete facts are known concerning the occurrence of *L. l. armata* and its relationship to immediately overlying faunas in this part of China, a final decision concerning the Series boundary cannot be given. However, the present evidence seems to favour the drawing of the boundary at some point within the *Blackwelderia sinensis* Zone rather than at its base as has so often been suggested. This conclusion pertains only to the Hwangho faunal facies belt. *Lejopyge* is yet unknown in this facies and is seemingly restricted to the Chiangnan Fauna. It is critical that further studies be conducted to find areas of intertonguing of the two faunal belts to prove or negate the above conclusion.

U.S.S.R. Three zones, namely the *Agnostus pisiformis*-*Homagnostus fecundus*, *G. stolidotus*, and *G. reticulatus* Zones constitute the early upper Cambrian Tuorski or Tuorian Stage, Siberian Platform (Table 3). Its stratotype occurs in the foothills of the Tuora-Sis Ridge, 6 km below Chekurovka village on the River Lena (Lazarenko 1966; Ivshin and Pokrovskaya 1968). In northern Siberia Demokidov (1968) has referred to the interval covered by the two lower zones as the Sukhanski Horizon. The middle-upper Cambrian boundary is drawn between the Mayanian (= Maisky) Stage and the overlying Tuorian Stage (Table 3). The uppermost zone of the Mayanian Stage is the Zone of *L. armata*-*Lomsucaspis alta* (Table 3). In Lazarenko's zonal scheme the same zone is called the Zone of '*L. armata*-*M. mirabilis*'. Presumably, *L. l. armata* is not necessarily present, as in the accompanying faunal list '*Lejopyge* ex gr. *laevigata*' is cited. However, elsewhere in Siberia *L. l. armata* has been recorded from many sections, for example in northern Siberia (Demokidov 1968) and in the north-western portion of the Siberian Platform, within the upper levels of the Mayanian Stage, in the Gremyakinskaya Anticline and on the River Mokoutey at

the Rynninskii Ledge (Datsenko *et al.* 1968). Note also that only *A. cf. pisiformis* has been recorded from the Altay-Sayan fold belt (Romanenko 1972), so it seems invalid to use it as one of the nominate species in a zonal scheme. '*Homagnostus fecundus*', however, is not yet described and is a *nomen nudum* (Lazarenko, pers. comm. 1974).

The faunal lists for the two oldest zones of the Tuorian Stage stratotype given by Lazarenko (1966, chart opposite p. 34) and by Ivshin and Pokrovskaya (1968, pp. 98–99) are significantly different. It is difficult to make a judgement without figures of the listed species and one might assume that the later of the two lists has updated the earlier one and includes taxa from more recent collections. With this in mind the following comments are offered. Four of the species listed for the *A. pisiformis*-'*H. fecundus*' Zone occur outside the limits of the U.S.S.R. In Sweden *Damesella(?) eremita* (= *Drepanura eremita* Westergård) and *Proceratopyge nathorsti* Westergård are known only from the *A. pisiformis* Zone whereas *Acrocephalites stenometopus* (Angelin) is confined to the *L. laevigata* Zone (Westergård 1952 and Table 2 herein). However, in her determination of fossils from the *G. stolidotus* Zone, Lazarenko (1966) identified *A. stenometopus agnostorum* Westergård and if this is correct, then the Swedish *A. pisiformis* Zone is indicated (Westergård 1948). Lazarenko (pers. comm. 1974) has not only reaffirmed the identification but has pointed out that the subspecies is now known from the *A. pisiformis*-'*H. fecundus*' Zone as well as the lower *G. stolidotus* Zone. We presume that *Acrocephalites stenometopus* recorded in Ivshin and Pokrovskaya (1968) is in reality the subspecies *A. s. agnostorum* in which case the base of the *A. pisiformis*-'*H. fecundus*' Zone will coincide with the middle-upper Cambrian boundary. If, however, *Acrocephalites stenometopus* is really present below *A. s. agnostorum*, then the middle-upper Cambrian boundary would need to be drawn within the zone and not at its base as indicated in Table 3 herein. The fourth species *Pseudagnostina contracta* was described by Palmer (1962) from the *G. stolidotus* beds in Alabama, U.S.A., where it is unknown outside that zone. In the Tuorian Stage stratotype *P. contracta* and *Proceratopyge nathorsti* pass from the *A. pisiformis*-'*H. fecundus*' Zone into the overlying interval referred to as the *G. stolidotus* Zone thus suggesting that the upper levels of the *A. pisiformis*-'*H. fecundus*' Zone may correlate with the lowest parts of the *G. stolidotus* Zone elsewhere. Such an idea is expressed in Table 3. It should also be emphasized that Ivshin and Pokrovskaya (1968, p. 98) recorded *G. reticulatus angelini* Resser and *Homagnostus obesus* (Belt) in the *G. stolidotus* Zone in addition to the nominate species. In Sweden *H. obesus* is confined to the *Olenus* Zone. Thus it appears that the upper part of the Siberian *G. stolidotus* Zone in the Tuorian Stage stratotype already includes rocks that can be correlated with the lower levels of the Swedish *G. reticulatus* Zone and consequently the upper boundary of the Siberian *G. stolidotus* Zone is drawn a little higher than the base of the Swedish *G. reticulatus* Zone (Table 3).

In the middle section of the River Kulyumbe, a tributary of the River Yenisey in north-western Siberia, the listed Swedish agnostids given in Datsenko *et al.* (1968, 'Atlas', Table 3, pp. 6–7) suggests that the Mayanian Stage, as recognized in that region, is represented by the time interval equivalent to that covering the Swedish Zone of *Ptychagnostus punctuosus* to the top of the *L. laevigata* Zone (but see below). Its two uppermost zones are the Zone of *Maiaspis spinosa*-*Oidalagnostus trispinifer* below and the Zone of *Acrocephalella granulosa*-*Koldiniella proluxa* above. All the

species in the latter zone are endemic to the U.S.S.R. except for *Peronopsis insignis* (Wallerius) which in Sweden is confined to the upper part of the *L. laevigata* Zone (Westergård 1946, p. 43). Rosova (1964, fig. 2) has indicated that *P. insignis* is restricted to the lower and midsections of the Sakhaiski Horizon, the uppermost division of the Middle Cambrian in her stratigraphic scheme. As well, Datsenko *et al.* (1968, p. 7) included *P. insignis* in their list of fossils contained in the *Acrocephalella granulosa-Koldiniella proluxa* Zone which together with the upper levels of the underlying *Maiaspis spinosa-Oidalagnostus trispinifer* Zone they equated with the Sakhaiski Horizon. However, on their charts Datsenko *et al.* (1968, fig. 31, p. 31) and Lazarenko and Nikiforov (1968, chart opposite p. 20) have also shown the occurrence of *P. insignis* in the very basal part of the overlying *Pedinocephalina-Toxotis(?)* Zone (Table 4). This seems to support the observation by Lazarenko and Datsenko (1967, chart opposite p. 16) of the presence of *P. insignis* in both the *A. granulosa-K. proluxa* and *Pedinocephalina-Toxotis(?)* Zones. Like Westergård (1946) we regard *P. insignis* as indicative of a late middle Cambrian age. However, in our opinion the agnostid figured as *P. insignis* by Lazarenko and Nikiforov (1968, pl. 1, figs. 1-5) is incorrectly assigned because the pygidial axes of the two forms are different and the glabella of the Swedish form is shorter than the Siberian form; likewise for the pygidium figured by Rosova (1964, pl. 13, fig. 16). Also Lazarenko and Nikiforov (1968) charted *Clavagnostus sulcatus* Westergård (known in Sweden only from the upper part of the *L. laevigata* Zone) as occurring above the form they called *P. insignis* (Table 4). The pygidia figured as *C. sulcatus* (Lazarenko and Nikiforov, pl. 3, figs. 13, 14) may be incorrectly assigned (Jago and Daily 1974, p. 99). Thus neither of these two agnostids are important for the boundary problem. However, their ranges are shown herein on Table 4 for comparison with those of other trilobites mentioned in the text.

Many of the species recorded in the *A. granulosa-K. proluxa* Zone range up from the underlying zone. Among the new forms is '*Homagnostus fecundus*' Pokrovskaya, the nominate zone fossil in the Siberian *A. pisiformis-H. fecundus* Zone of the type Tuorian Stage. Datsenko *et al.* (1968) have indicated on their stratigraphic tables (p. 7 and Table 13, p. 41) that the *A. granulosa-K. proluxa* Zone at the top of their Mayanian Stage is middle Cambrian in age. However, as the Swedish agnostid *O. trispinifer* ranges only to the top of the *M. spinosa-O. trispinifer* Zone (Table 4), we suggest that the middle-upper Cambrian boundary should be placed at the top of this zone (Table 3) rather than at the top of the succeeding *A. granulosa-K. proluxa* Zone as suggested by most Soviet workers. Also because of the spot occurrence of '*H. fecundus*' in the latter zone (Table 4) the present authors suggest that this zone would better equate with the *A. pisiformis-H. fecundus* Zone of the type Tuorian Stage, in which case it is upper Cambrian in age (Table 3).

The lower levels of the overlying Zone of *Pedinocephalina-Toxotis(?)* can be correlated with the lower Nganasanski Horizon at the bottom of the Kulyumbeiski Superhorizon or Substage of Rosova (1963, 1964, 1968, 1970) by means of the short-ranging *Nganasanella nganasanensis* Rosova, *Koldiniella convexa* Lazarenko, and *Groenwallina decora* Rosova (Tables 3 and 4). *Pseudagnostus nganasanicus* Rosova occurs in the same horizon (Rosova 1964, fig. 2). Also of importance for correlation is the reported occurrence of the very distinctive *Acidaspidella limita* Rosova, the

lower range of which according to Rosova (1964, 1968, 1970) is near the base of the Nganasanski Horizon, although Datsenko *et al.* (1968, 'Atlas', fig. 31, p. 31) and Lazarenko and Nikiforov (1968, chart opposite p. 20) record its first appearance above the upper range of *N. nganasanensis*. Rosova's observations for the species' range are accepted herein (Table 4) particularly as Rosova (1970) has re-emphasized its occurrence near the base of the Nganasanski Horizon. *P. nganasanicus* and *A. limita* appear to be endemic to the U.S.S.R. Their occurrence also in the *G. stolidotus* Zone of the Tuorian Stage stratotype (Ivshin and Pokrovskaya 1968) permit reference of both the lower Nganasanski Horizon and the lower part of the *Pedinocephalina-Toxotis*(?) Zone to the *G. stolidotus* Zone. Such a conclusion reinforces the view suggested above that the *A. granulosa*-*K. prolixa* Zone is to be correlated with the *A. pisiformis*-*H. fecundus*' Zone of the Tuorian Stage stratotype and with the lower part of the Swedish *A. pisiformis* Zone (Table 3).

CONCLUSIONS

The present revision of the taxonomic status of *L. cos* Öpik has led to the conclusion that it is a junior synonym of the morphologically variable *L. l. armata* Westergård. All known species of *Lejopyge* are of late middle Cambrian age.

In Sweden *L. laevigata* and its subspecies range through the *Solenopleura brachymetopa* Zone and throughout the succeeding Zone of *L. laevigata*, the top of which marks the middle-upper Cambrian boundary.

For Australia, it is advocated that because *L. cos* Öpik is synonymous with *L. l. armata* Westergård, the middle-upper Cambrian boundary should be drawn within the Mindyallan Stage and at a level within the *Cyclagnostus quasivespa* Zone between the *L. cos* and *Blackwelderia sabulosa* faunas. Previously the boundary has been drawn at the base of the Mindyallan Stage.

L. laevigata is presently unknown from British rocks. In England recent finds of agnostids and other fossils in the Merevale No. 3 Borehole show that the middle-upper Cambrian boundary lies within an unfossiliferous interval between the occurrence of *Hypagnostus sulcifer* (Wallerius), found near the top of the Mancetter Grits and Shales, and below the occurrence of *Agnostus pisiformis* (Linnaeus) and *Schmalenseeia cf. amphioneura*, found towards the base of the overlying Outwoods Shales (Table 3).

In North America the top of the *Bolaspidella* Assemblage Zone, which contains *L. calva*, has been regarded as the uppermost zone of the middle Cambrian. However, present evidence from Alaska where both *L. calva* and *L. laevigata* are found, suggests that the middle-upper Cambrian boundary for North America is more likely to occur within the overlying *Cedaria* Zone (Table 3).

In China *L. laevigata* is apparently absent within the shallow-water shelf facies of the Hwangho Faunal Facies belt. Existing evidence favours the positioning of the middle-upper Cambrian boundary at some undefined level within the *Blackwelderia sinensis* Zone rather than at its base. However, elsewhere in China and within the Chiangnan Faunal Facies belt, the occurrence of *L. l. armata* and other cosmopolitan agnostids should permit a reliable positioning of the Series boundary.

On the Siberian Platform, in the foothills of the Tuora-Sis Ridge, the middle-upper

Cambrian boundary appears to be correctly drawn between the *L. l. armata-Lomsucaspis alta* Zone below, and the *A. pisiformis-Homagnotus fecundus* Zone above. However, in north-west Siberia evidence presented above suggests that the middle-upper Cambrian boundary should be drawn at the top of the *Maiaspis spinosa-Oidalagnostus trispinifer* Zone (Table 3) rather than at the top of the succeeding *Acrocephalella granulosa-Koldiniella prolixa* Zone as is presently done by Soviet authors.

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